



Management and Conservation Article

Effects of Experimental Canopy Manipulation on Amphibian Egg Deposition

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ABSTRACT Although effects of forest management on amphibians are relatively well studied, few studies have examined how these practices affect egg deposition by adults, which can impact population recruitment. We quantified the effects of 4 canopy tree-retention treatments on amphibian oviposition patterns in clusters of 60-L aquatic mesocosms located in each treatment. We also related aquatic and terrestrial biophysical parameters in treatment plots to oviposition patterns. Cope's gray treefrogs (*Hyla chrysoscelis*) deposited more egg masses in clear-cut and 25–50% tree-retention treatments than in controls. In contrast, mountain chorus frogs (*Pseudacris brachyphona*) deposited more egg masses in unharvested control and 75% retention treatments than in clear-cut or 25–50% retention treatments. Spotted salamanders (*Ambystoma maculatum*) only deposited eggs in 75% retention treatments and controls. The number of egg masses deposited by mountain chorus frogs was positively related to canopy cover and negatively related to water temperature, pH, and dissolved oxygen, whereas we noted the opposite relationships for Cope's gray treefrogs. We did not detect a relationship between the number of egg masses deposited by any species and the distance of mesocosms to either the nearest mature closed-canopy forest or to the nearest natural amphibian breeding pool. The impacts of the silvicultural treatments we studied were species-specific and depended on the amount of trees removed. In areas where protection of spotted salamander and mountain chorus frog breeding habitat is a priority, we recommend harvests retain at least 75% of the canopy. Our results also suggest that retention of 25–50% of canopy trees surrounding amphibian breeding pools has little conservation benefit.

KEY WORDS *Ambystoma maculatum*, amphibians, clear-cut, Cumberland Plateau, forestry, *Hyla chrysoscelis*, oviposition, *Pseudacris brachyphona*, silviculture.

Forest managers are increasingly interested in considering the impacts of silviculture on biodiversity (Lindenmayer and Franklin 2002). The response of amphibians to forest management has received much attention (deMaynadier and Hunter 1995, Semlitsch 2003) because this vertebrate group is sensitive to habitat disturbance and population declines are occurring worldwide (Stuart et al. 2004, Patrick et al. 2006). Management activities that reduce forest canopy can lead to lower survival rates, higher extinction probabilities, and smaller body sizes of postmetamorphic amphibians (Rothermel and Semlitsch 2006, Todd and Rothermel 2006, Harper et al. 2008). These demographic changes may contribute to reduced abundance of amphibians in clear-cuts (Renken et al. 2004, Patrick et al. 2006). Additionally, adult amphibians may avoid clear-cuts or heavily harvested areas because they are inhospitable for movement (Gibbs 1998, Chan-McLeod 2003). Thus, a combination of fewer breeding adults and reduced habitat permeability within harvested sites could result in fewer eggs deposited.

Amphibians have evolved mechanisms to select oviposition sites where the survival of their offspring is maximized (Resetarits and Wilbur 1989, 1991). In addition to factors such as the presence of conspecifics and predators (Resetarits and Wilbur 1989, Petranks et al. 1994), water depth (Crump 1991), and potential of infection by pathogens (Kiesecker and Skelly 2000), canopy cover is known to influence choice of

oviposition site (Binckley and Resetarits 2007). Pools with open canopy are preferred over pools with closed canopy by ovipositing Cope's gray treefrogs (*Hyla chrysoscelis*), squirrel treefrogs (*Hyla squirrel*), and gray treefrogs (*Hyla versicolor*; Binckley and Resetarits 2007, Hocking and Semlitsch 2007). Thus, certain species may benefit from canopy reduction associated with timber harvesting.

Quantifying how the degree of timber harvest influences the number of egg masses deposited by different amphibian species is fundamental to prescribing forest management techniques that are sensitive to this declining vertebrate group (Marzluff et al. 2000). Accordingly, we studied aquatic mesocosms in experimental forest stands to determine how different levels of canopy tree removal affected egg deposition of pool-breeding amphibians in the southern Cumberland Plateau region of Alabama, USA. Our objectives included quantifying patterns of oviposition and the response of biophysical conditions in and around mesocosms located in forest stands subjected to a gradient of canopy tree-retention treatments. We also tested for relationships between these biophysical parameters, distance to mature forest, and number of egg masses to explore possible mechanisms responsible for observed patterns of oviposition.

STUDY AREA

Our study area was located in Jackson County, Alabama, USA. The area was in the Cliff section of the Cumberland Plateau in the mixed mesophytic forest region and in the Northern Cumberland Plateau section of the Eastern

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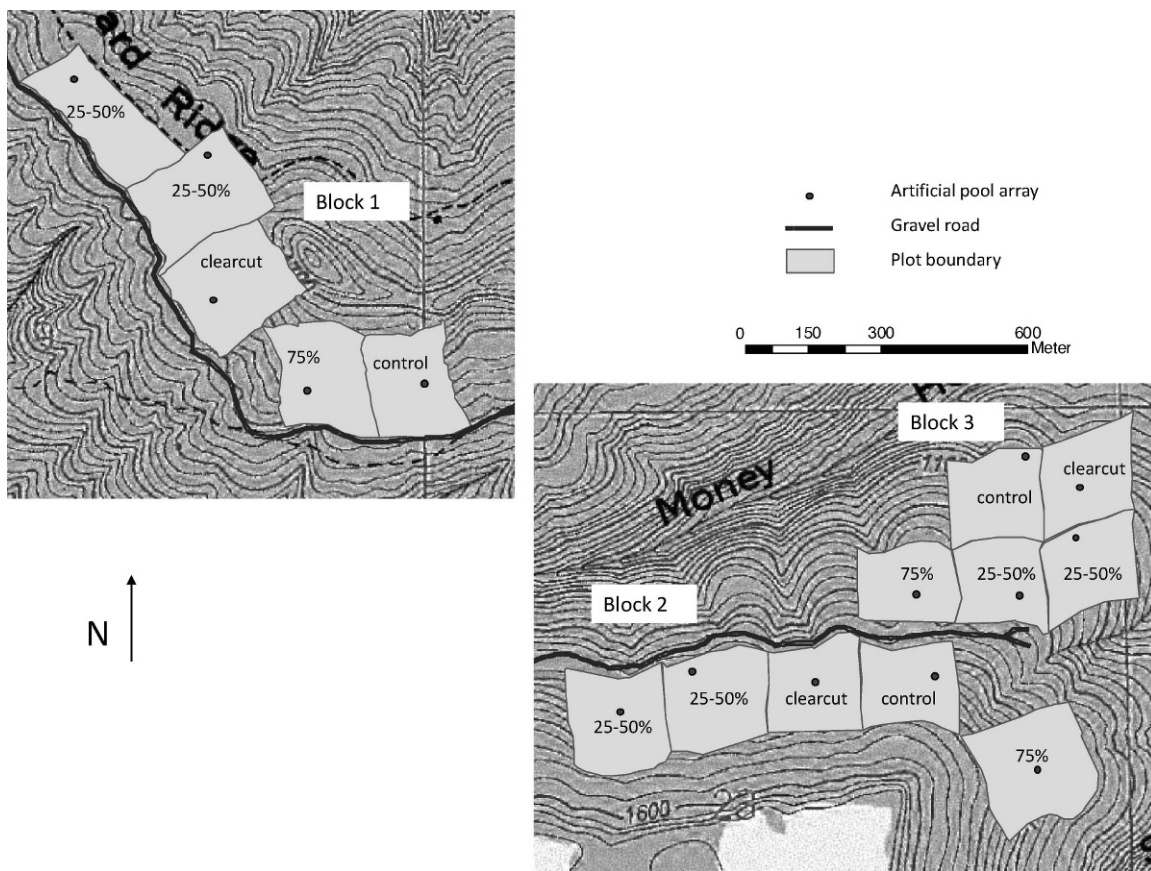


Figure 1. Randomized complete block design for canopy tree-retention treatments showing location of aquatic mesocosm arrays, Jackson County, Alabama, USA, 2004 and 2005. Block 1 was located 13 km west-northwest of Blocks 2 and 3.

Broadleaf Forest (Oceanic) Province (Braun 1950, Bailey et al. 1994). The area was characterized by steep slopes dissecting the plateau surface and draining to the Tennessee River. Soils were shallow to deep, stony and gravelly loam or clay, well drained, and formed in colluvium from those on the plateau top (Smalley 1982). Climate of the region was temperate with mild winters and moderately hot summers with a mean temperature of 13° C and mean precipitation of 149 cm (Smalley 1982). We conducted our study at 2 sites: one site was located on a south-southwest-facing slope of Miller Mountain (34°58'11"N, 86°12'21"W) and the other was located on a north-facing slope at Jack Gap (34°56'30"N, 86°04'00"W). Dominant canopy tree species were oaks, including black oak (*Quercus velutina*), northern red oak (*Quercus rubra*), white oak (*Quercus alba*), and chestnut oak (*Quercus prinus*), which comprised 46% of pretreatment basal area (BA). Hickories (*Carya* spp.; 15% pretreatment BA), sugar maple (*Acer saccharum*; 13% pretreatment BA), and yellow poplar (*Liriodendron tulipifera*; 9% pretreatment BA) also were present. Common understory species included flowering dogwood (*Cornus florida*), eastern redbud (*Cercis canadensis*), and sourwood (*Oxydendrum arboreum*).

METHODS

We used a randomized complete block design with one block located at Miller Mountain (elevations 457–518 m)

and 2 blocks at Jack Gap (elevations 304–475 m). Each block had 5 4-ha experimental units: 2 plots with 25–50% BA retention treatment and one plot each of clear-cut, 75% retention, and control treatments (Fig. 1). The clear-cut and 25–50% retention treatments were chainsaw-felled and grapple-skidded in a commercial logging operation. In the 25–50% retention treatments, we marked favorable dominant and codominant trees that displayed high vigor, especially oak, ash (*Fraxinus* spp.), and persimmon (*Diospyros virginiana*). In 75% retention plots, we killed the mid-story by incising trees (\bar{x} = 566 trees/ha, SD = 39; \bar{x} = 7.4 cm dbh) with intermediate and suppressed crowns (Smith et al. 1997) and applying the herbicide Arsenal® (active ingredient imazapyr; BASF Corp., Ludwigshafen, Germany) to retain a nearly intact canopy without large gaps but allow increased light penetration to the forest floor. We harvested trees in October and November 2001 and March 2002 and applied herbicide in November 2001. In August and September 2002, we measured posttreatment BA in the treatment plots and verified that the approximate retention rate per treatment was achieved (control: \bar{x} = 22.7 m²/ha, SD = 1.6 [99% retention]; 75% retention plots: \bar{x} = 23.6 m²/ha, SD = 1.6 [70% retention]; 25–50% retention plots: \bar{x} = 8.6 m²/ha, SD = 3.1 [38% retention]; and clear-cut: \bar{x} = 1.2 m²/ha, SD = 1.8 [5% retention]). We designed these treatments to determine the most efficacious silvicultural prescription for regenerating oak forests, and subse-

quently used them to study wildlife response (Schweitzer 2003, Wang et al. 2006). Although we did not obtain pretreatment data for amphibians, we assumed distributions and abundances of amphibians were similar across our plots prior to applying treatments because of the close proximity of sites, random assignment of treatments, and the uniform forest structure. Pretreatment BA did not differ across treatments (Schweitzer 2003).

Within each experimental unit, we installed a group of 3 aquatic mesocosms within 5 m of the perimeter of a randomly chosen vegetation measurement plot that was used in another study (Schweitzer 2003). All mesocosms were ≥ 50 m from the edge of the experimental unit (range = 50–119 m; \bar{x} = 87.3 m, SD = 25.8; Fig. 1). Mesocosms were 60-L black plastic mortar tubs ($91 \times 61 \times 46$ cm) arranged in a triangular fashion approximately 1.5 m apart and buried flush with the ground. We installed pools in September 2002 and allowed them to fill with rainwater. To simulate ephemeral conditions of local wetlands and reset environmental conditions in mesocosms, we dried each pool for at least 14 days each year by hand-bailing water during late October of 2002, 2003, and 2004. Natural pools found on or near the study site were also generally small in size and dried annually similar to our mesocosms.

Between April and September 2003, we examined the presence of amphibian eggs every 7–14 days (\bar{x} = 9 days) to assess amphibian colonization and use of pools. In 2004 and 2005, we expanded sampling and counted number of egg masses from February through October. We based survey frequency on hatching time for species to avoid recounting eggs: mountain chorus frog (*Pseudacris brachyphona*) eggs hatch in 7–10 days (Mitchell and Pauley 2005), Cope's gray treefrog eggs hatch in 3–5 days (Ritke et al. 1990), and American toad eggs (*Anaxyrus americanus*) hatch in 3–12 days (Green 2005). Spotted salamander (*Ambystoma maculatum*) eggs took longer to hatch but were large enough in size and in small enough numbers that we easily noticed the addition of new eggs to mesocosms between surveys. Though we took these precautions, it is possible that we recounted some eggs of each species; however, we assume that the likelihood of recounting was similar among treatments. We counted egg masses as groups of 40–50 eggs for each species, similar to the method used by other authors, except for American toads (Hocking and Semlitsch 2007). For this species, we considered each individual string of eggs a mass. We used a range of eggs to define an egg mass because of the difficulty in obtaining a precise count of eggs within an egg mass, and because egg masses frequently fall apart after oviposition. Thus, although our egg mass estimates may not represent true abundance, comparison among treatments is relevant because we counted egg masses consistently. We carried out our research under Alabama Department of Conservation of Natural Resources collecting permit number 4144.

We monitored biophysical parameters within pools once per month February–August 2004 and October–November 2004, and March–June 2005 and August–September 2005. In each pool, we measured pH with an Oakton pH Testr

probe (Oakton Instruments, Vernon Hills, IL), water temperature ($^{\circ}$ C) and dissolved oxygen (DO; ppm) using a YSI DO200 probe (YSI Inc., Yellow Springs, OH) at a depth of 10 cm. In September 2004 and 2005, we estimated canopy cover >2 -m height over each pool array using a spherical densiometer held at chest level. We used a handheld Global Positioning System unit and digital orthophoto quarter-quadrangle imagery in a Geographic Information System to determine the distance from aquatic mesocosms to the nearest edge of mature, closed-canopy forest (i.e., control and 75% retention treatments or untreated areas outside study plots), and distance to nearest natural amphibian breeding pool.

We averaged all biophysical variables and totaled egg mass number for each experimental unit for 2004 and 2005. We calculated average pH by first converting pH to H^{+} ion concentration, averaging the H^{+} ion concentrations, and then converting H^{+} back to pH. To test for year and treatment effects on mean total number of egg masses and biophysical variables (water temperature, DO, pH, canopy cover), we used a mixed model (PROC MIXED in SAS; SAS Institute Inc., Cary, NC) with treatment and block as main factors, year as a repeated factor, and Tukey's Honestly Significant Difference tests for mean separation. We included block in the model to remove the potential confounding effects of site variation. We square-root-transformed egg mass count data and arcsine-transformed canopy cover data; transformed data met normality and equal variance assumptions (Kolmogorov–Smirnov and Levene Statistic, respectively, $P \geq 0.05$). When an interaction occurred between year and treatment, we analyzed years separately using analysis of variance (ANOVA) with treatment and block as main factors.

We used linear regression to test for a relationship between egg mass number and distance to nearest mature forest edge in clear-cut and 25–50% retention treatments and between egg mass number and distance to nearest natural breeding pool. To explore the relationship between oviposition and biophysical conditions in pools, we used principal components analysis to reduce the original 4 variables to a single principal component (PC). We assessed the PC analyses using a Kaiser–Meyer–Olkin measure of sampling adequacy (KMO) test of sampling adequacy, which measures the degree of common variance among the original variables, and Bartlett's test of sphericity, which tests the null hypothesis that the original variables are not intercorrelated (Hair et al. 2005). We then used simple linear regression to test relationships between egg mass number and scores for the biophysical PC. Because of interannual variation, we ran these analyses separately for 2004 and 2005. We performed regression analyses only on species that occurred in all 4 treatments in a given year, which were Cope's gray treefrog and mountain chorus frog. We performed statistical analyses in SAS 9.1 at $\alpha = 0.05$.

RESULTS

Four species of amphibians deposited eggs in our aquatic mesocosms: Cope's gray treefrog, mountain chorus frog,

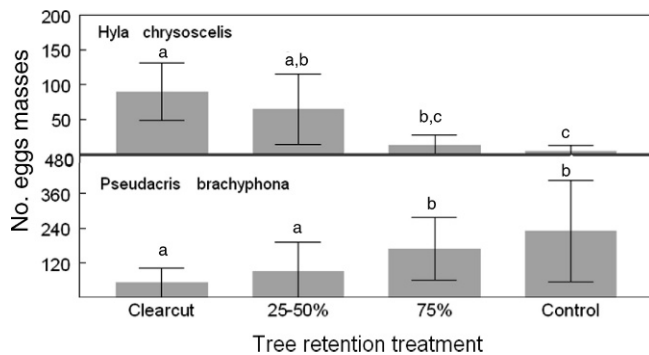


Figure 2. Mean egg mass counts for Cope's gray treefrog (*Hyla chrysoscelis*) and mountain chorus frog (*Pseudacris brachyphona*) ovipositing in aquatic mesocosms located in 4 tree-retention treatments, Jackson County, Alabama, USA, 2004 and 2005. Unlike letters above bars are statistically different ($P < 0.05$) by repeated-measures mixed model and Tukey's Honestly Significant Difference test.

spotted salamander, and American toad. By fall 2003, egg masses were deposited in 97% ($n = 44$) of mesocosms. Egg deposition in treatments differed among species. We observed American toad egg masses only in the 25–50% and 75% retention treatments, whereas spotted salamanders deposited eggs only in the 75% retention treatments and controls. Because of the resulting unbalanced design (i.e., some treatments with no egg deposition), we did not test for statistical differences among treatments for these species but interpret their results qualitatively.

For Cope's gray treefrogs and mountain chorus frogs, we did not detect interactions between year and treatment ($F_{3,11} = 0.83\text{--}1.03$, $P = 0.42\text{--}0.50$). Cope's gray treefrogs deposited more egg masses in the clear-cut and 25–50% retention mesocosms than in controls, and this species deposited more in the clear-cut than in 75% retention mesocosms ($F_{3,9} = 6.34$, $P = 0.01$; Fig. 2). Mountain chorus frogs deposited more egg masses in control and 75% retention mesocosms than in the 25–50% retention and clear-cut treatments ($F_{3,11} = 6.85$, $P = 0.007$; Fig. 2), and this species deposited more egg masses in 2005 than 2004 ($F_{1,11} = 84.9$, $P \leq 0.001$).

The number of egg masses deposited in 25–50% and clear-cut treatment plots by Cope's gray treefrogs and mountain chorus frogs were not related to distance to nearest mature forest ($n = 9$, $R^2 = 0.03\text{--}0.12$, $P = 0.36\text{--}0.68$). Number of egg masses deposited for either species was not related to distance to the nearest natural breeding pool ($n = 14\text{--}15$, $R^2 = 0.06\text{--}0.11$, $P = 0.23\text{--}0.40$).

Mesocosm pH was higher in the clear-cut and 25–50% retention treatments than in the control ($F_{3,9} = 4.11$, $P = 0.04$; Fig. 3), and higher in 2005 than 2004 ($F_{1,11} = 5.14$, $P = 0.04$). Dissolved oxygen was higher in mesocosms in clear-cut and 25–50% treatments than in 75% retention and control mesocosms ($F_{3,9} = 7.38$, $P = 0.009$; Fig. 3). We detected an interaction between year and treatment for both canopy cover and water temperature ($F_{3,11} = 4.57\text{--}4.62$, $P = 0.02\text{--}0.03$). Canopy cover was highest in the 75% retention and control treatments and lowest in clear-cuts in 2004 ($F_{3,9} = 29.20$, $P \leq 0.001$), and it was higher in

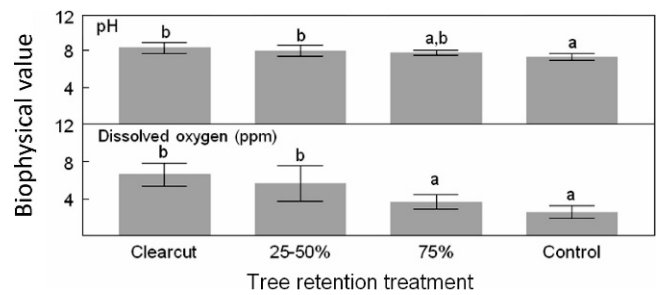


Figure 3. Mean pH and dissolved oxygen in aquatic mesocosms located in 4 tree-retention treatments, Jackson County, Alabama, USA, 2004 and 2005. Unlike letters above bars are statistically different ($P < 0.05$) by repeated-measures mixed model and Tukey's Honestly Significant Difference test.

controls than in clear-cuts in 2005 ($F_{3,9} = 4.70$, $P = 0.03$; Fig. 4). Water temperature was highest in clear-cuts and lowest in controls in 2004 ($F_{3,9} = 9.16$, $P = 0.004$), and it did differ among treatments in 2005 ($F_{3,9} = 3.39$, $P = 0.07$; Fig. 4).

The 4 biophysical variables were reduced to one PC with 72% and 88% retention of original variance in 2004 and

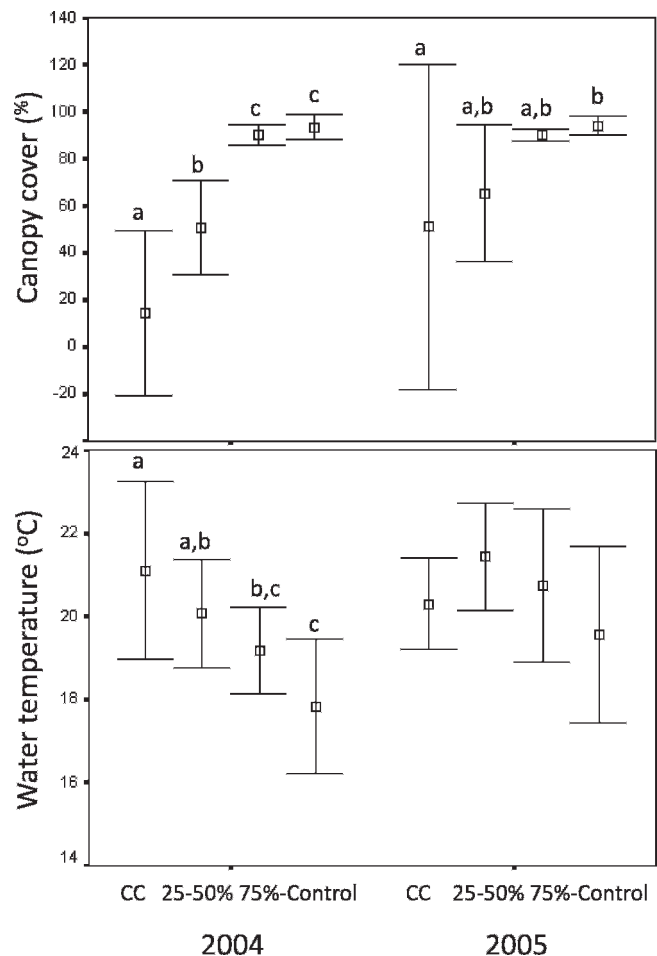


Figure 4. Mean canopy cover and water temperature in aquatic mesocosms located in 4 tree-retention treatments, Jackson County, Alabama, USA, 2004 and 2005. Unlike letters above bars are statistically different ($P < 0.05$) by analysis of variance and Tukey's Honestly Significant Difference. CC = clear-cut; percentages represent tree-retention treatments.

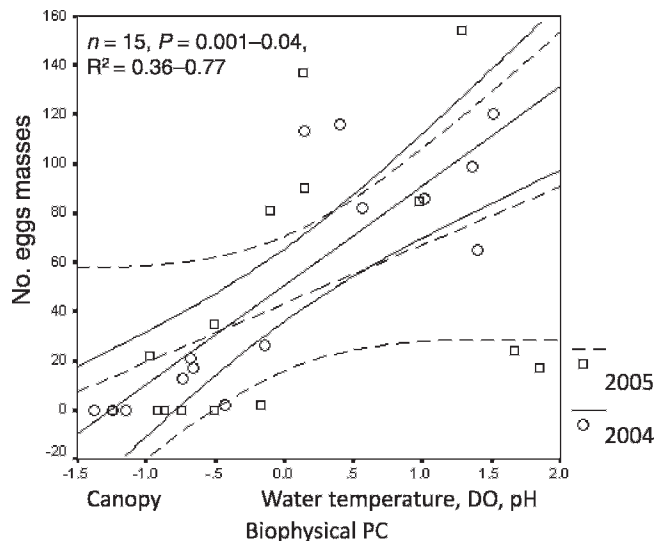


Figure 5. Number of Cope's gray treefrog (*Hyla chrysoscelis*) egg masses versus average biophysical principal component (PC) score at 15 aquatic mesocosms located across a forest canopy gradient in Jackson County, Alabama, USA, 2004 and 2005. Based on PC loadings, large negative values indicate a high percentage of canopy and large positive values indicate high water temperature, dissolved oxygen, and pH.

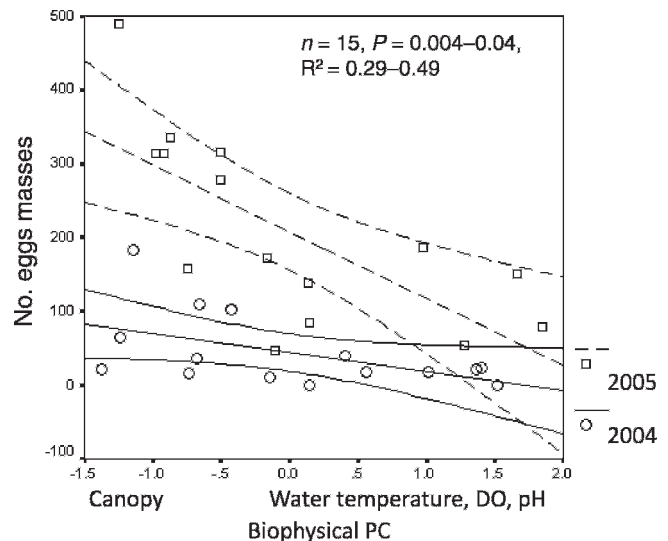


Figure 6. Number of mountain chorus frog (*Pseudacris brachyphona*) egg masses versus average biophysical principal component (PC) score at 15 aquatic mesocosms located across a forest canopy gradient in Jackson County, Alabama, USA, 2004 and 2005. Based on PC loadings, large negative values indicate a high percentage of canopy and large positive values indicate high water temperature, dissolved oxygen, and pH.

2005, respectively (KMO measure of sampling adequacy = 0.79–0.80, Bartlett's test of sphericity $\chi^2 = 28.0$ –56.5, $P \leq 0.001$). The first PC verified ANOVA results—canopy cover was negatively correlated with water temperature, DO, and pH in both years. Indeed, as canopy cover decreased and water temperature, DO, and pH increased, the number of Cope's gray treefrog egg masses increased ($n = 15$, $R^2 = 0.29$ –0.77, $P = 0.001$ –0.04; Fig. 5). In contrast, as canopy cover decreased and water temperature, DO, and pH increased, the number of mountain chorus frog egg masses decreased ($n = 15$, $R^2 = 0.29$ –0.49, $P = 0.004$ –0.04; Fig. 6).

DISCUSSION

Silvicultural treatments involving removal of canopy trees had species-specific effects on oviposition by amphibians. The average number of mountain chorus frog egg masses was 4–6 times lower in clear-cuts compared to 75% retention cuts and controls. In contrast, the average number of Cope's gray treefrog egg masses was 8–15 times greater in clear-cuts compared to 75% retention cuts and controls. Spotted salamanders did not oviposit in clear-cut and 25–50% retention cuts whereas American toads deposited eggs only in 75% and 25–50% retention cuts. Canopy removal affected microhabitat conditions within mesocosms and led to an increase in pH, DO, and water temperature. Species-specific trends in oviposition likely were related to differences in preference for these microhabitats or possibly habitat permeability.

Our results agreed with previous findings of a preference by ovipositing Cope's gray treefrogs for open-canopy versus closed-canopy pools (Binckley and Resetarits 2007, Hocking and Semlitsch 2007). Survival was higher and time to

metamorphosis was lower for Cope's gray treefrog tadpoles in clear-cuts compared to forests, possibly due to higher and more optimal water temperatures in clear-cuts for this species (Hocking and Semlitsch 2008). In our study, mesocosms in harvested plots had the highest water temperature, DO, and pH—all factors that can positively influence growth and survival of tadpoles (Noland and Ultsch 1981, Werner and Glennemeier 1999, Skelly et al. 2002, Halverson et al. 2003). Mean water temperature in clear-cuts and 25% retention cuts was around 21° C, which is within the ideal temperature range (20–25° C) for embryo and larval development of most amphibians in temperate regions that breed in pools during late spring and summer, such as the Cope's gray treefrog (Duellman and Trueb 1986, Wells 2007). Cope's gray treefrogs also may have been attracted to vegetation type around our mesocosms. Although we did not measure vegetation directly, there was more herbaceous vegetation around mesocosms in clear-cuts and 25% retention cuts, conditions that gray treefrogs prefer at breeding sites (Binckley and Resetarits 2007, Hocking and Semlitsch 2007).

In contrast, mountain chorus frogs and spotted salamanders may have selected mesocosms in the closed-canopy treatment pools because of optimal biophysical parameters for their development. These species breed earlier in the year and may have preferentially selected pools where water temperatures were cooler. The ideal temperature range for embryo and larval development of most amphibians in temperate regions that breed in pools during early spring tends to be lower (<20° C) than species that breed later (Duellman and Trueb 1986, Wells 2007). Mean water temperature in control plots was <20° C both years. Similar to Cope's gray treefrogs, pool selection by mountain chorus

frogs and spotted salamander also may have been related to preference of the surrounding vegetation. Spotted salamanders prefer habitats associated with forested wetlands at multiple scales, from preferences for forest substrates over grassland substrates to positive relationships between the area of upland forests surrounding breeding pools and both probability of occurrence and population size (Homan et al. 2004, Rittenhouse et al. 2004, Skidds et al. 2007). Lastly, mean DO was lower in closed-canopy treatments; however, it did not drop below levels (<1.5 ppm) known to negatively affect embryo and larval development (Branch and Taylor 1977, Wells 2007).

American toads are found in a variety of habitats including dense forest, old field, prairie, or suburban areas (Green 2005). In Maryland, American toads use forested habitats more often than open fields and were most frequently found under dense canopy cover (Forester et al. 2006). Ovipositing female American toads, however, strongly prefer open-canopy to closed-canopy pools, suggesting that toads may tend to deposit eggs in areas with some level of canopy removal (Werner and Glennemeier 1999).

It is possible that differences in egg deposition may have been related to vagility (Gibbs 1998, Rothermel and Semlitsch 2002, Chan-McLeod 2003). Adult mountain chorus frogs and spotted salamanders may have perceived canopy openings or clear-cuts as viscous environments, hence they may not have ventured into these treatment plots to find suitable breeding sites. Spotted salamanders show a strong behavioral avoidance of open grassy habitats (Rittenhouse and Semlitsch 2006). In contrast, Cope's gray treefrog may have traveled farther into open-canopy treatments. Our mesocosms were located 50–119 m from the treatment edges, and there was no relationship between number of eggs deposited and distance to mature forest. Hocking and Semlitsch (2007) reported that female gray treefrogs deposited eggs more frequently in pools positioned 10 m into clear-cuts compared to those at 50 m, but use by male gray treefrogs was not affected by distance to mature forest. Although we did not test the effect of mesocosm position on oviposition rates, our results suggest that Cope's gray treefrogs may travel over 50 m into open habitats to find breeding sites.

It is also possible that habitat preference and movement capability interact with timing of oviposition. Species that breed later in the season, such as Cope's gray treefrog, may oviposit based on the distribution of species that have already bred (e.g., spotted salamander and mountain chorus frog) to avoid larval competition (Wilbur 1984, Resetarits and Wilbur 1989, Petranks et al. 1994). It is also possible that Cope's gray treefrog egg masses were consumed by spotted salamander or mountain chorus frog larvae residing in closed-canopy mesocosms before we could count them, thereby inflating the positive effect of canopy removal on oviposition of this species. The spotted salamander can be a significant egg predator (Savage and Zamudio 2005).

Because we were interested in natural oviposition rates, we did not cover our mesocosms to prevent colonization by invertebrates. Aquatic invertebrates are known predators of

amphibian eggs and larvae; thus if colonization differed among treatments, number of detected egg masses could have been confounded (Morin 1983, Gunzburger and Travis 2004). We recorded the presence of invertebrate taxa in mesocosms and did not find any meaningful relationships between invertebrate colonization and number of egg masses (Z. Felix, Alabama A&M University, unpublished data). In 2004 and 2005, we observed adult backswimmer beetles (Family Notonectidae, Order Coleoptera) at least once in 17% of mesocosms arrays in 25–50% retention treatments, in 67% of arrays in 75% retention treatments, and in 33% of control arrays. We observed larval dragonflies (Order Odonata) at least once in 17% of 25–50% and 75% retention treatment arrays, and in 33% of clear-cut arrays. Other studies have reported increased prevalence of dragonflies in open- versus closed-canopy pools (McCauley 2005, Hocking and Semlitsch 2008). Increased abundance of larval dragonflies in clear-cuts compared to mature forest habitats had little effect on survival of gray treefrog tadpoles in Missouri (Hocking and Semlitsch 2008). It is unlikely that higher prevalence of dragonfly larvae in open-canopy treatments affected mountain chorus frog and spotted salamander oviposition because these amphibian species breed prior to dragonflies and we dewatered all pools between years.

MANAGEMENT IMPLICATIONS

We suggest that reducing canopy cover below 25% has little negative impact on Cope's gray treefrogs and possibly other species with similar breeding habitat preference. Thus, harvests that reduce 75% or more of the forest canopy may be an effective conservation strategy to restore Cope's gray treefrog populations. In areas where conserving spotted salamander and mountain chorus frog is a priority, we recommend that harvests retain at least 75% of the forest canopy. We also suggest that American toads prefer sites with intermediate canopy exposure (25–75%).

We recommend that future studies investigating the impacts of forest harvesting on amphibian populations use a before–after control–impact (BACI) design (Smith 2002). The BACI design uses pre- and posttreatment data to quantify treatment effects, and thus it can take into consideration differences in pretreatment species distribution. Additional research also is needed on the fate of larvae and recently metamorphosed amphibians among canopy removal treatments (e.g., Patrick et al. 2007, Hocking and Semlitsch 2008, Rittenhouse et al. 2008). Studying the impacts of forest harvesting on all age classes is the only way that strong inferences can be made on wildlife impacts (Marzluff et al. 2000).

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